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**Nest defence and predator recognition by Arctic tern
(*Sterna paradisaea*)**

Master thesis

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Annotation:

In the presented work, I describe the behaviour of Arctic terns (*Sterna paradisaea*) toward predator species that differ in the threat they represent to them and to their nests. I presented textile dummies of great black-backed gull (*Larus marinus*), peregrine falcon (*Falco peregrinus*), common raven (*Corvus corax*) and common eider (*Somateria mollissima*), piece of wood as a harmless stimulus, and human intruder in sitting position near the tern nests. Experiments were conducted on the Varanger peninsula in Norway. The tern behaviour was recorded and analysed to see any dummy species related differences.

I hereby declare that I have worked on my master thesis independently and used only the sources listed in the bibliography.

In České Budějovice, 7th December 2022

Jan Špička

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1 Introduction

Antipredatory behaviour is an essential skill for every animal species to ensure survival and increase fitness. There are multiple forms of behaviour shown under the threat of predation; the most pronounced ones are those performed during the nest defence (Caro 2005). The bird nest is defenceless, and very valuable for the parents; therefore, an intensive antipredatory behaviour of the parents importantly increases the nest survival and therefore their own fitness (Montgomerie & Weatherhead 1988). Birds use a myriad of diverse strategies to protect their nests from predators; from the positioning of the nest, and its inconspicuousness, to the physical defence executed by the parents (Mainwaring et al. 2014).

During the physical defence of the nest, the parents put themselves at considerable risk when attacking the predator. They may be captured or injured as a result of risky manoeuvres during their attacks on the predator. It is a very energy- and time-consuming activity, which threatens the lives of parents. Therefore, it is important to correctly identify the predator and assess the threat it poses (e.g., Strnadová et al. 2018).

Several studies have shown that birds are capable of distinguishing a predator from a harmless species. Tvardíková & Fuchs (2012) showed that great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), marsh tits (*Poecile palustris*) and willow tits (*Poecile montanus*) distinguish threatening sparrowhawk (*Accipiter nisus*) and kestrel (*Falco tinnunculus*) from harmless pigeon and thrush. Moreover, birds can assess the threat each predator species represents (Curio et al. 1983). E.g., Kleindorfer et al. (2005) showed that reed warblers (*Acrocephalus* sp.) are able to dynamically assess the threat posed by the predator according to its distance from nest or the position of the nest itself relative to the ground, as the low nests are threatened more by terrestrial predators and high nests by aerial predators.

The evidence for precise predator recognition combined with threat assessment is not numerous. For example, red-backed shrikes (*Lanius collurio*) hesitate to attack Eurasian sparrowhawk, while being very aggressive to common kestrel both being very similar small raptors. The reason for this difference in behaviour is the extreme threat, which the sparrowhawk represents for the adults, while the kestrel threatens rather the chicks (Strnad et al. 2012). Similar evidence is shown in a study that observes the feeder attendance by titmice. Tvardíková & Fuchs

(2011) showed that tits attend the feeder more often in the presence of kestrels, as they are less skilled in capturing small passerines than sparrowhawks, suggesting that titmice are less scared of the kestrel than the sparrowhawk.

The specific type of predator is human that represents a great threat to animals, both intentionally and unintentionally. Most animals usually lack the ability to defend themselves from such a large intruder. When threatened by humans, birds often produce alarm calls (Shen et al. 2020) or dive at the intruder on some occasions (Knight et al. 1987). A different strategy is used by the lesser golden plover (*Pluvialis dominica*). This species is trying to distract human intruder from its nest by pretending injury (Byrkjedal 1989).

However, obtaining comprehensible behaviour requires an easy-to-read performance of the parents during the nest defence. Terns are known for their very aggressive and vigorous nest defence. Most often they need to fend off avian predators such as gulls and skuas, but they usually do not hesitate to attack even much larger predators such as Arctic fox (*Vulpes lagopus*), polar bear (*Ursus maritimus*), as well as humans (Fuchs 1977, Burger et al. 1993, Palestis 2005). Although, Clode et al. (2000) suggested that Arctic terns react distinctively to various mammalian intruders, the extent to which tern aggression is associated with particular predator species remains unclear.

In the present study, we observe the nest defence behaviour of the Arctic tern (*Sterna paradisaea*) population in the northernmost parts of Europe, Varanger peninsula, Norway. We presented dummies of predators varying in the level of threat they represent to the parents and the eggs in the nest to test if the vigorous antipredatory behaviour of terns is adaptive and reflects the perceived threat. We compared the responses to avian intruders with the human sitting at the nest. Personal observations suggest that arctic terns vigorously attack humans passing close to their nests, aiming their attacks at the highest point of the intruder (usually the head), and occasionally embellishing with precisely aimed defecation, which usually forces the human to retreat.

We tested the following hypotheses:

- 1) Arctic terns show stronger antipredatory behaviour in the presence of threatening species than control stimuli.
- 2) Human is considered as a threatening stimulus.
- 3) Arctic terns show stronger antipredatory behaviour in the presence of species that threaten the clutch than species that threaten adults.

2 Material and Methods

2.1 Study species

The Arctic tern is a small species of the Laridae family (Charadriiformes) that feeds almost exclusively on fish. It is well known for its migratory behaviour, as it performs the world's longest migration, from their breeding grounds in the Arctic all the way to the Antarctica to its wintering grounds (Hromádková et al. 2020). Terns usually breed in colonies, but a small proportion of their population breed solely (Bergman 1980). The terns build a simple nest of small stones and lay 1–3 eggs that are incubated for 21 days (Mallory et al. 2017). After breeding, they embark on the journey to Antarctica in late August to early September (Hromádková et al. 2020).

2.2 Study area

The experiments were carried out on the south-east coast of Varanger peninsula, Norway (N 70.18347, E 30.32919). The Arctic tern colonies were scattered along the coast to the east, always within one kilometre (often much less) from a village. Therefore, we expect that terns have some experience with human intruders near their nests. We have conducted our experiments on the nests at the edge of colonies or at solitary nests to prevent large numbers of birds from engaging in antipredatory behaviour.

The ground nests of Arctic terns are vulnerable to predation. At our study locality, the most common predators of nests are red fox (*Vulpes vulpes*), gulls, skuas, and corvids. According to the European Bird Breeding Atlas (Keller et al. 2020), in our study area (grid no. 36WVC1) there are low hundreds of breeding great black-backed gull (*Larus marinus*), tens of breeding pairs of Arctic skua (*Stercorarius parasiticus*), long-tailed skua (*Stercorarius longicaudus*) and common raven (*Corvus corax*) and individual breeding pairs of gyrfalcons (*Falco rusticolus*) and peregrine falcon (*Falco peregrinus*) threatening especially the adult terns.

2.3 Stimuli

We chose species that differ in the threat they represent to the nest and to the adult birds. There were four dummies prepared from textile and coloured with acrylic paint (see Němec et al. 2015 for justifying this method, Fig. 1): a) great black-backed gull – predator of eggs and chicks nor of the adults; b) common raven – predator of eggs and chicks nor of the adults; c) peregrine falcon – predator of the adult terns; d) common eider (*Somateria mollissima*) – harmless duck. Also, we presented a human figurant sitting on the ground dressed in black cloth and a piece of wood the same size as the dummies as a baseline.



Figure 1: Presented stimuli, from the left: great black-backed gull (*Larus marinus*), peregrine falcon (*Falco peregrinus*), common raven (*Corvus corax*), common eider (*Somateria mollissima*), and wooden log. All stimuli are displayed at the same scale.

2.4 Experiment

After finding the nest we noted its GPS coordinates and assessed the stage of incubation using a water test (as described in van Paassen et al. 1984). We conducted the experiments on the clutches during their second half of the incubation. The dummy was always brought to the nest concealed by a piece of black cloth, placed 2 metres away from the nest, and facing toward the nest. The dummy (as well as the human and wood) remained concealed until the tern calmed down and sat on his nest. If the tern refused to sit, the experiment has commenced after ten minutes if the tern was present at least. Subsequently, the cloth was pulled away by a string revealing the dummy. After ten minutes of the dummy exposure, the field assistant approached the dummy concealing it with the cloth and retreated with it from the nest. We have scheduled one-hour breaks between stimuli to let the tern calm down and incubate. The six stimuli were

presented at each experimental nest in random order, except for the human, which was always the last stimulus, therefore, each nest was disturbed for approximately seven hours.

2.5 Statistical analyses

We have conducted the experiment on 13 nests and despite the possibility that there could be more terns present during the experiment in the nest surrounding; we evaluated only the reaction of one focal pair of terns belonging to the experimental nest. Terns were not individually marked, but we determined the identity of the focal pair according to their responses, as they were significantly more active than any other present tern. However, we included the number of terns present during the experiment in subsequent data analyses (see below).

For statistical analyses, we used seven behavioural responses. 1) Number of attacks executed during the experiment. We always recorded an attack when the tern flew towards the stimulus, descending in the flight height and ascending in the close proximity to the stimulus (approx. 50 cm). The attack may or may not be associated with physical contact with the stimulus and/or defecation. 2) Number of flyovers, i.e., inspection flights above/over the stimulus without an apparent decrease in the flight height. 3) Number of flights outside the stimulus position. One flight was determined by a change in direction of the flight. 4) Total distance in meters flown during the entire experiment. 5) Total time in seconds spent near the stimulus up to a range of 15 meters. 6) Total time in seconds spent outside the range of 15 meters from the stimulus. 7) Total time in seconds spent sitting on the nest (incubation).

To obtain a composite behavioural response, we utilized principal component analysis (PCA). This multivariate approach enabled to show the correlation of behavioural responses, to normalize and standardize the response data, and to obtain a canonical response variable describing the antipredatory behaviour.

The variability in the canonical response variables (Gaussian distribution) was explained using a linear mixed effect model (command `lmm` in the R package `lme4`) with the bird ID nested in the nest ID (random slope model) coded as random factors. We created two models, one for the canonical scores of the first PCA axis and the second for the canonical scores of the second axis. We included the latency (in seconds) until the focal birds calm down after being disturbed by the experimenter installing the stimulus at their nest as a covariate in both models to control for individual variability in the overall bird sensitivity to disturbance. We included three predictor

variables in each model: the stimulus type (gull, falcon, raven, eider, human, log), the order of the experiment (first to sixth, coded as categorical variable), and the number of birds involved in the antipredatory behaviour during the experiment (coded as continuous variable). We used stepwise forward selection, and we compared particular models using the likelihood ratio test (Chi squared test). To compare the values of the categorical predictors, we used the Tukey HSD post hoc test (z test, command `glht` in the R package `multcomp`) with Tukey correction for multiple comparisons.

3 Results

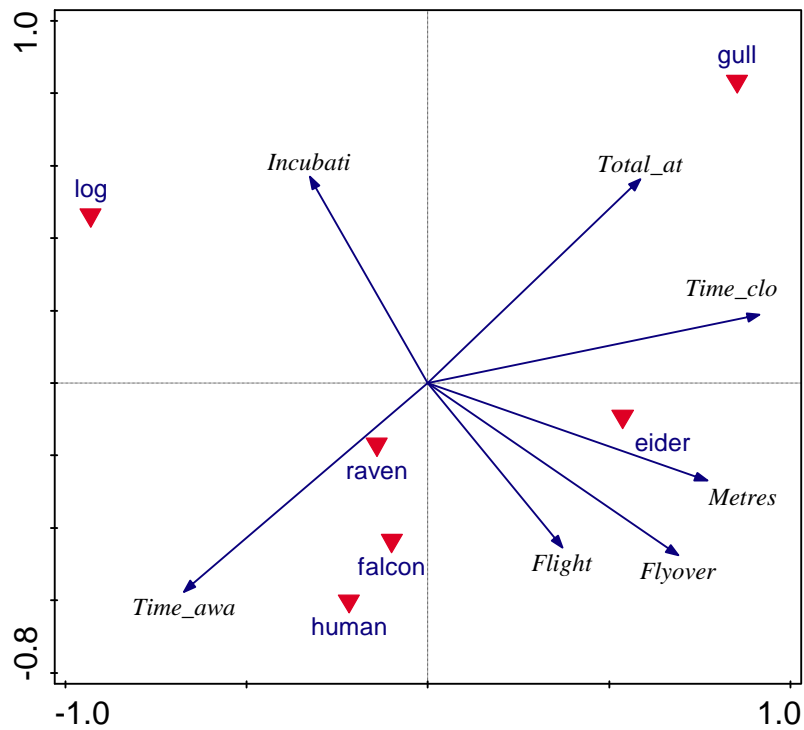


Figure 2: Visualization of first two canonical axes of Principal Component Analysis of all recorded behaviours of arctic terns in the presence of particular stimuli. Flyover – number of flights above the stimulus, Metres – total distance flown during the experiment, Time_clo – total time spent in the distance of less than 15 meters from the stimulus/nest, Total_at – number of attacks to the stimulus, Flight – number of flights outside the stimulus, Time_awa – total time spent outside the range of 15 meters from the stimulus, Incubati – total time spent sitting on the nest.

3.1 First canonical axis

The first canonical axis of the principal component analysis explained 42.2 % of the variability of the behavioural data (Fig. 2). In the negative values, it was loaded especially by the time spent more than 15 meters away from the dummy during the experiment (Time_awa, loading -0.675). In positive values, it was loaded by the total time spent at a distance less than 15 meters from the stimulus/nest (Time_clo, loading 0.915), total metres flown during the experiment (Metres, loading 0.771), number of flights over the dummy (Flyover, loading 0.691), and total number of attacks (Total_at, loading 0.587).

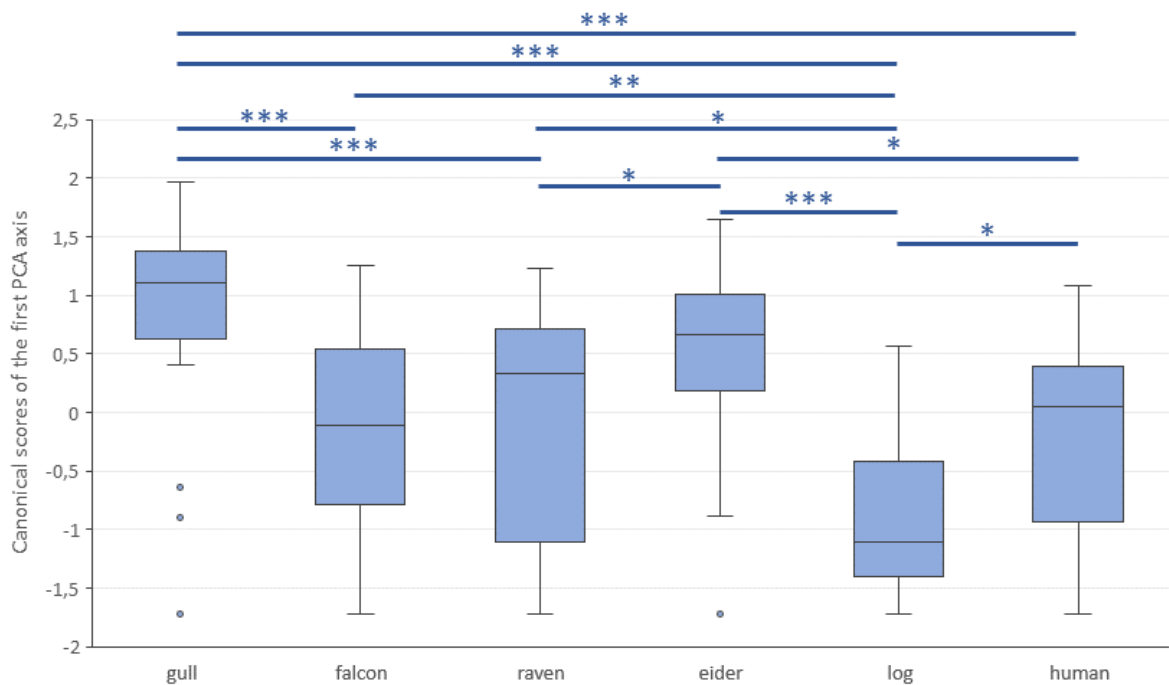


Figure 3: Canonical scores of the first PCA axis obtained in experiments presenting particular stimuli. Box represents 75 % quantile, whiskers 95 % quantile, the horizontal line within the box is median, and the dots are outliers.

The variability in the canonical scores of the first PCA axis was significantly affected by the stimulus presented (Tab. 1). The gull dummy scored the highest values, meaning that it was most often attacked, the terns spent the most time in its proximity, flew the most meters, and performed many flights over as well as away from the gull dummy. On the contrary, they avoided sitting on the nest. The intensity of the reaction to the gull dummy was significantly higher than toward the baseline control stimulus, the wooden log (post hoc Tukey HSD test,

$t = 7.691$, $p < 0.001$; Fig. 3), falcon dummy (post hoc Tukey HSD test, $t = 4.107$, $p < 0.001$; Fig. 3), raven dummy (post hoc Tukey HSD test, $t = 4.285$, $p < 0.001$; Fig. 3), and human figurant (post hoc Tukey HSD test, $t = 4.617$, $p < 0.001$; Fig. 3) but it did not differ from the responses to the eider dummy (post hoc Tukey HSD test, $t = 1.360$, $p = 0.751$; Fig. 3).

Table 1: Effects of predictor variables in two linear mixed-effect models constructed. Order – order of the trial (first to sixth), in which the stimulus was presented, Number of birds – Number of birds involved in nest defence, F – F values, DF – degrees of freedom. Significant effects are in bold.

<i>Response</i>	<i>Predictor</i>	<i>F</i>	<i>DF</i>	<i>P</i>
<i>First axis scores</i>	Stimulus	14.574	5	<<0.001
	Order	0.445	4	0.776
	Number of birds	24.190	1	<0.001
<i>Second axis scores</i>	Stimulus	9.981	5	<0.001
	Order	0.953	4	0.435
	Number of birds	0.495	1	0.483

Another stimulus eliciting a lot of excitement in the arctic terns was the eider dummy. The responses to eider were significantly stronger than towards the wooden log (post hoc Tukey HSD test, $t = 6.331$, $p < 0.001$; Fig. 3), raven dummy (post hoc Tukey HSD test, $t = 2.925$, $p = 0.045$; Fig. 3), and human figurant (post hoc Tukey HSD test, $t = 3.257$, $p = 0.017$; Fig. 3). There is a marginal difference in the reaction compared to the falcon dummy (post hoc Tukey HSD test, $t = 2.748$, $p = 0.072$; Fig. 3) but there is no difference from the gull dummy, as mentioned above.

The responses to the falcon dummy, the raven dummy and the human figurant did not differ significantly from each other (post hoc Tukey HSD tests, falcon – raven: $t = 0.177$, $p = 0.999$; falcon – human: $t = 0.510$, $p = 0.996$; raven – human: $t = 0.333$, $p = 0.999$; Fig. 3), but differ significantly from the control stimulus – wooden log (falcon – log: $t = 3.583$, $p = 0.006$; raven – log: $t = 3.406$, $p = 0.011$; human – log: $t = 3.073$, $p = 0.030$; Fig. 3). Terns often spent a lot of time further from the dummy and observed the stimuli from greater distances (20–50 metres).

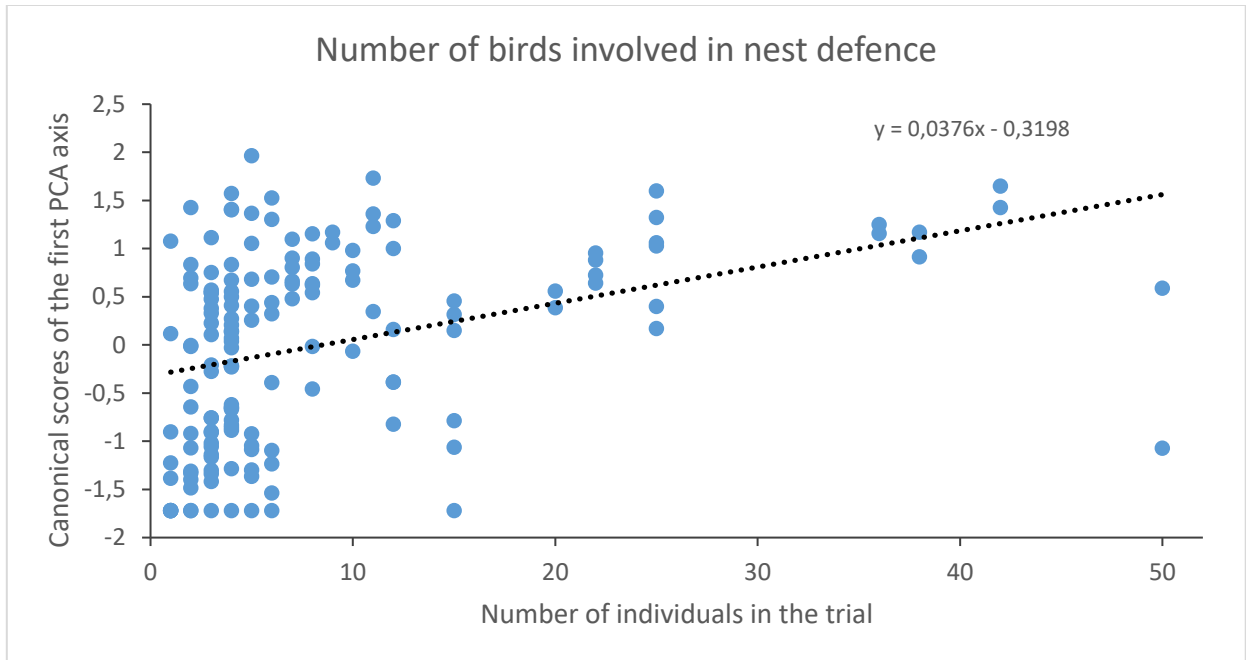


Figure 4: Effect of the number of birds involved in the nest defence on the canonical scores of the first PCA axis obtained in experiments presenting all stimuli. The black line represents the linear regression of the data, the equation describes the slope of the line.

We did not show a significant effect of the order, in which the stimulus was presented (Tab. 1), but we showed a significant effect of the number of birds involved in the nest defence during particular trials (Tab. 1). The more birds engaged in antipredatory behaviour, the stronger and more active was the response of each individual bird (Fig. 4).

3.2 Second canonical axis

The second canonical axis of the principal component analysis explained 21.6 % of the variability of the behavioural data (Fig. 2). In the negative values, it was loaded by the number of flights away from the dummy (Flight, loading -0.454); in the positive values, it was loaded by the time spent sitting on the nest (Incubati, loading 0.569) and attacking the dummy (Total_att, loading 0.563).

The variability in the canonical scores of the second PCA axis was significantly affected by the stimulus presented (Tab. 1). Gull dummy scored the highest values, meaning that the terns were often close to it (and attacking). Followed by the log, which was also often approached, and the terns incubated the clutch. The reaction to the gull dummy differs significantly from that of eider, falcon, raven, and human (post hoc Tukey HSD tests, $t = 3.776$, $p = 0.003$; $t = 5.176$,

$p < 0.001$; $t = 4.090$, $p < 0.001$; $t = 5.858$, $p < 0.001$ respectively, Fig. 5). Furthermore, the reaction to the log differs significantly from falcon and human (post hoc Tukey HSD tests, $t = 3.669$, $p = 0.004$; $t = 4.350$, $p < 0.001$ respectively, Fig. 5).

We did not show significant effect of the order in which the stimulus was presented, or the number of birds involved in the nest defence on the variability of the canonical scores of the second axis (Tab. 1).

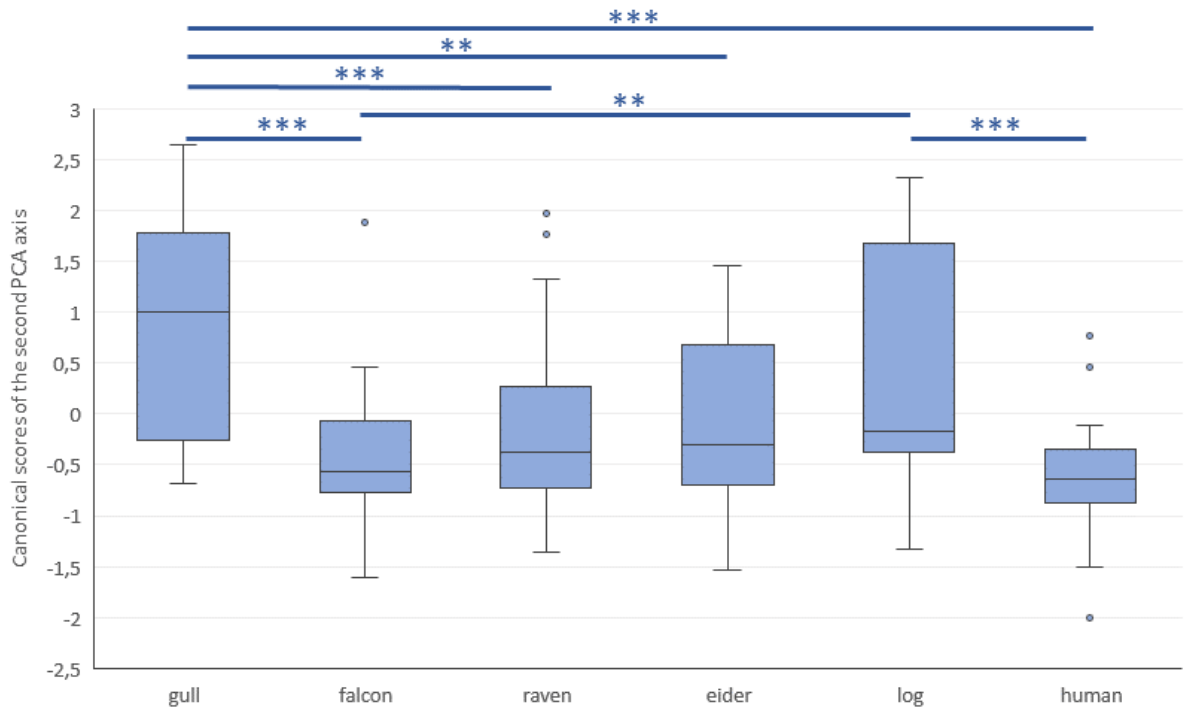


Figure 5: Canonical scores of the second PCA axis obtained in experiments presenting particular stimuli. Box represents 75 % quantile, whiskers 95 % quantile, the horizontal line within the box is median, and the dots are outliers.

4 Discussion

Arctic terns showed the most intense antipredatory behaviour towards the dummy of a black-backed gull. Antipredatory behaviour included vigorous attacks – often with physical contact, numerous flights over the dummy, consequently terns have flown a great distance. Terns performed this behaviour in the presence of a gull dummy more often than in trials with other dummies. This suggests that gull represents a threat to the nest (eggs), and adult terns consider the gull as nonthreatening to themselves and easy to chase away from the nest using mobbing

behaviour. This is in concordance with Burton & Thurston (1959), Jackson & Key (1992), and Palestis (2005) who showed that terns attack gulls commonly.

Raven, falcon and human elicited also more antipredatory behaviour than the baseline stimulus (wooden log), suggesting that they are considered as threat. Ravens can have a great impact on ground-nesting birds, as they often predate their eggs or chicks (Andrén et al. 1985, Coates & Delehanty 2010). The Falcon poses a great threat to adult terns since birds of similar size appear regularly in its diet (Drewitt & Dixon 2008). Bradley & Oliphant (1991) even found remains of two Arctic tern individuals in falcon pellets. Human represents a threat through disturbance of adult incubating birds, as the eggs may cool down rapidly as the adult bird is scared away by humans (Syrová et al. 2020). Furthermore, a human can accidentally step on the nest because it is very inconspicuous.

Contrary to our predictions, eider also elicited a strong antipredatory response. Even stronger than in the case of raven, falcon, and human. Eider does not eat terns or their eggs as it is believed to be specialized on marine invertebrates especially bivalves (Cantin et al. 1974, Merkel et al. 2007). It may represent a threat in case when it accidentally crashes the eggs. The antipredatory response to the eider was seemingly the same as that to the gull. Nevertheless, the second canonical axis of our multivariate analysis showed a significant difference between these two dummies, suggesting that the eider was attacked by some terns, but they rather spent more time by flying over it, and very often, they were also far from the dummy. Therefore, we suggest that particular terns differ considerably in their attitude to the eider, likely because of their individual experience.

The responses to falcon and human were very similar at both axes. The terns usually flew away from the nest and observed the stimulus from a distance of 20 to 50 metres. This response differs from both, the baseline stimulus as well as from the gull, the main nest predator. Our explanation is that terns fear both these stimuli and/or do not feel capable of chasing them away from the nest. This is not surprising in the case of the falcon, which is extremely threatening for adult birds. Walters (1990) showed that, blacksmith lapwings (*Vanellus armatus*) register falcons from a great distance, and they try to escape and hide rather than attract attention.

Thus, we were able to show that Arctic terns have the capacity to evaluate the threat that particular predator species represent. This was previously shown in Siberian jays (*Perisoreus*

infaustus; Griesser 2009), red-backed shrikes (Ash 1970, Strnad et al. 2012), killdeer (*Charadrius vociferus*; Brunton 1990), and various other bird species (see Fuchs et al. 2019 for a review). Similarly, Cavanagh & Griffin (1993) showed that common terns attack landing gulls and ignore those, who are just flying over, since the landing gull could be preparing for predatory act.

We predicted terns actively mobbing humans, according to existing studies (Burger & Gochfeld 1991, Syrová et al. 2020). In our experiments, we almost did not observe any attacks on a human figurant sitting at the tern's nest. But before the experiment, as we were walking in the colony, attacks were frequent. We conclude that terns consider sitting figurant scary and large object that cannot be forced away. There is a certain level of experience of our study tern population with humans, as there was always a small settlement within a couple hundred metres from the colony. However, humans tend to avoid tern colonies.

The response to the raven contrasts with the response to the gull. Both these species are specialized to bird nest plundering (Stiehl & Trautwein 1991, Veitch et al. 2016), so we expected equal responses of terns. There was also quite variable response to raven dummy, some pairs stayed away from it, but some guarded it, and some even attacked it. We may consider that the terns differ in their individual experience with the raven as a threat. Ravens are not as abundant as gulls at our study location (Keller et al. 2020), and moreover, in the high arctic, ravens may utilize other abundant food sources, especially carcasses (Stahler et al. 2002, Matley et al. 2012, Chevallier et al. 2016). Consequently, the predation pressure of ravens in our tern population may be significantly weaker than that of gulls.

To conclude, we were able to show that terns are not fanatical aggressors attacking any object near their nests. Contrariwise, they perform a complex behavioural response to different predators. This response reflects the threat that predators pose to both nest content and parent birds. Terns can thus effectively chase away predators, which can be chased away; while do not spend energy and do not threaten themselves during mobbing threatening predators.

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